

PROTEOID ROOTS IN THE SOUTH AFRICAN PROTEACEAE

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ABSTRACT

The 54 representative species of Proteaceae examined had abundant proteoid roots and it is concluded that they are normal components of the root systems of all 13 genera in southern Africa. Proteoid root terminology is revised and extended in view of the predominance of compound types in fynbos vegetation. Their relative contribution to the root system may reach up to 80 % total root dry weight but varies between individuals and species, and with plant age, season, soil type and location of parent roots in the soil profile. While proteoid-root formation is usually dependent on soil water availability, the presence is reported of "anomalous" young proteoid roots on *Leucospermum hypophyllocarpodendron* during summer drought. The number of rootlets may reach 650 per 10 mm length of parent root providing, together with their long root hairs, a substantial increase in surface area available for absorption of water and nutrients. There is, however, no simple relationship between abundance of proteoid roots and plant weight, at least in the first few years of growth.

UITTREKSEL

PROTEOÏDE WORTELS IN DIE SUID-AFRIKAANSE PROTEACEAE

Die 54 verteenwoordigende soorte Proteaceae ondersoek, het volop proteoïde wortels en word die gevolgtrekking gemaak dat dit normale komponente van al 13 genera in Suidelike Afrika is. Proteoïde terminologie is hersien en uitgebrei in die lig van die oorwegend saamgestelde tipes in fynbos-plantegroei. Hulle relatiewe bydrae tot die wortelsisteem mag soveel as 80 % droë gewig wees maar dit verskil tussen individuë en soorte en met die ouderdom van plante, seisoen, en die posisie van die ouer-wortel in die grondprofiel. Alhoewel die proteoïde-wortelvorming afhang van die beskikbaarheid van grondwater, word die teenwoordigheid van "afwykende" jong proteoïde wortels by *Leucospermum hypophyllocarpodendron* gedurende somerdroogte vermeld. Die aantal worteltjies kan tot 650 per 10 mm lengte ouer-wortel oplewer wat met die lang wortelhare 'n betekenisvolle vermeerdering in oppervlakte beskikbaar vir absorpsie van water en voedingstamme is. Daar is egter geen eenvoudige verhouding tussen die voorkoms van proteoïde wortels en plantge-
wig nie, ten minste nie gedurende die eerste paar groeijare nie.

INTRODUCTION

Proteoid roots are dense clusters of rootlets in longitudinal rows (Fig. 1), and were first described for the family Proteaceae in Australia by Purnell (1960) and elaborated on by Lamont (1972a). Until recently, the South Afri-

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can literature on the Proteaceae was devoid of references to these structures (e.g. van Staden, 1968) though Vogts (1960) clearly alluded to them in her priority-for-research question "... why the superficial roots are so extremely sensitive and whether the presence of mycorrhizae is necessary to continued development." Proteoid roots are not mycorrhizal but are now considered analogous in their function (Lamont, 1982). More recently, Pathmaranee (1974) and Lamont (1981a), both in Australia, recorded some cultivated South African species with proteoid roots. In South Africa, Low (1980) has also made preliminary records from field excavations in the Cape, though proteoid roots were not observed on all plants, and van Staden *et al.* (1981) considered the rootlets of *Protea neriifolia* which formed in tissue culture were proteoid. The aim of this project was to examine representatives of the full range of South African Proteaceae for proteoid roots. By quantitative studies it was also hoped to obtain information on their relative morphology, contribution to the root system, occurrence in the field, factors controlling their formation and clues to their functional importance to the plant.

MATERIAL AND METHODS

Root systems were washed free of soil particles, separated into proteoid and non-proteoid root portions, and dried at 80°C for 48 h. For weighing purposes, even within compound proteoid roots, parent roots not bearing proteoid rootlets were considered non-proteoid. Morphological measurements were made with vernier calipers, often with the aid of a x10 dissecting microscope. Roots for electron microscopy were fixed in 70% alcohol, dehydrated in an alcohol-amyl acetate series, critical-point dried, gold-coated and scanned with a Jeol JB 35C electron microscope.

Nine-month plants referred to in the text were grown in two parts decomposed leaf litter: six parts siliceous gravel in plastic pots. They were drip-fed daily with tapwater and were 40% shaded in summer. Two-year cuttings were grown in two parts compost: one part loam: three parts sand in plastic bags. They were watered overhead with tapwater as required and kept in the open. Four-month seedlings of *Leucadendron laurum* under

FIG. 1.

Proteoid roots as viewed with scanning electron microscope. A, rootlets of mature proteoid root showing dense mat of root hairs up to their tips. B, rootlets of young proteoid root prior root hair development. C, proteoid rootlets just emerging in longitudinal rows from the parent root. D, surface view of mature proteoid root showing crowding of rootlets and their close association with soil particles (on the left). A-C = *Leucadendron salicifolium*, D = *L. laurum*. Scale: A = 1 mm, B-D = 100 μ m.

the previous treatment were transplanted into 2,5ℓ plastic pots containing either Clovelly sand from Pella via Atlantis or Hutton clay-loam from Jonkershoek. They were grown for a further 22 wk in a plastic greenhouse, watered with tapwater, and three random replicates of each were selected for root analysis.

RESULTS AND DISCUSSION

Taxonomic distribution

Table 1 shows that all specimens of all (54) species examined possessed proteoid roots (nomenclature follows the latest revision available). This included two *Aulax* species (three in genus), one *Brabejum* (one), three *Diastella* (five), two *Faurea* (five), ten *Leucadendron* (81), six *Leucospermum* (47), two *Mimetes* (16), one *Orothamnus* (one), two *Paranomus* (17), 12 *Protea* (83), eight *Serruria* (50), two *Sorocephalus* (11) and three *Spatalla* (20).

In association with what is already known about the proteoid-root bearing propensity of the sub-families Proteoideae (12 genera in South Africa) and Grevilleoideae (one genus in South Africa) (Lee, 1978; Lamont, 1981a), the results here suggest that proteoid roots are normal components of the root systems of all taxa in (southern) Africa. This is in contrast with Australia, where there are five genera lacking proteoid roots, especially in the primitive Persoonioideae. (The claim that *Agastachys* (Proteoideae) lacks proteoid roots (Lee, 1978) needs further investigation).

Expanded terminology

Following Purnell (1960), simple proteoid roots comprise a single cluster of rootlets (Fig. 2a). They are sometimes produced sequentially (in "series") along a parent root during the one growing season (Lamont, 1972a). Compound proteoid roots are defined here as a group of three or more clusters of rootlets borne on three or more parent roots (in "parallel"). The compound root therefore refers to a cluster of simple proteoid roots (Purnell, 1960: Fig. 2b). Clusters of rootlets are considered here to belong to separate compound proteoid roots if they are separated by more than one lateral root not bearing clusters of rootlets. Second order parent roots may arise from the axis of a primary proteoid root borne along the first order (original) parent root. This is defined here as a "closed" compound proteoid root. If the secondary proteoid roots arise from a non-proteoid portion of the parent root, the compound proteoid root is regarded as "open" (Fig. 2b). If only some of the second-order parent roots arise from a proteoid axis it is "incompletely-closed". If a primary proteoid root is present (usually terminal) but none of the second-order parent roots arise from it, the compound pro-

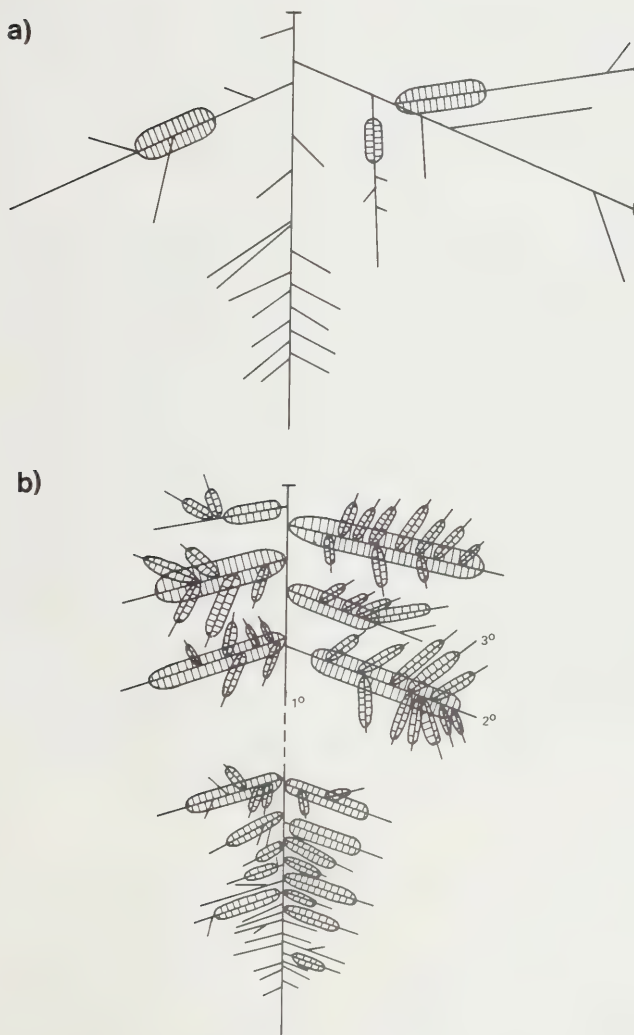


FIG. 2.

a. Part of a new season's lateral branch of *Serruria florida* with three simple proteoid roots. b. The same for *Leucospermum formosum* showing an "open" compound root with 28 second order (2°) parent roots and 111 simple proteoid root components (middle portion omitted). Note that all but two of the third order (3°) parent roots are "closed". Not drawn to scale.

teoid root is "incompletely-open". Tertiary and (the extremely rare) higher order proteoid roots are usually closed with respect to their parent roots, but otherwise the same terminology applies. For example, the compound proteoid roots of *Leucospermum formosum* are open or incompletely-open, with closed or incompletely-closed tertiary proteoid roots, and closed quaternary and quaternary proteoid roots (Fig. 2b).

Morphometrics

Returning to Table 1, all plants possessed at least some simple proteoid roots, with those of the genera containing the smallest plants, *Serruria*, *Sorocephalus* and *Spatalla*, remaining essentially simple throughout the life of the plant. Compound proteoid roots, usually open, were common in the other genera and contributed increasingly to the root system as plants increased in age (e.g. *Brabejum stellatifolium*, Table 1). Only *Leucospermum* and *Mimetes* were well represented by partly-closed, as well as open, compound proteoid-roots in mature plants, while most proteoid roots of *Orothamnus* were closed compound, though they were sparsely branched. The maximum number of second-order parent roots per compound proteoid root was 40 (*Leucospermum conocarpodendron*), with *Protea repens* having up to 35. Branching of compound proteoid roots was least in *Spatalla*, *Sorocephalus*, *Serruria* and *Faurea*. Individual proteoid roots tended to be smallest in *Spatalla*, *Paranomus* and *Faurea* (<35 mm long, <15 mm wide) and largest in *Leucadendron* and *Leucospermum* (<75 mm long, <35 mm wide). Older plants tended to have larger individual proteoid roots (e.g. *B. stellatifolium*, *Leucadendron lauratum*). The longest, simple proteoid root noted was 75 mm (*Leucospermum conocarpodendron*) and the shortest was 1.5 mm (*Spatalla racemosa* and *O. zeyheri*). The widest was 34 mm (*Leucospermum parile*) and the narrowest 1.4 mm (*Spatalla incurva*).

TABLE 1.

Occurrence and morphology of proteoid roots in 54 species of Proteaceae indigenous to southern Africa.

Species	Specimens	Description of proteoid roots			
		Type ⁺	No. of 2° rts*	Length (mm)	Width (mm)
<i>Aulax cancellata</i>	9 mth seedlings, sand-humus mix	S,O/C	—	5-30	—
<i>A. umbellata</i>	9 mth seedlings, sand-humus mix	SO	—	5-40	—
	Mature shrub, sandstone, Kogelberg	S,O,C	10	3-44	3-14

Species	Specimens	Description of proteoid roots			
		Type ⁺	No. of 2° rts*	Length (mm)	Width (mm)
<i>Brabejum stellatifolium</i>	2 yr seedlings, shale, Kirstenbosch	S,O	9	5-27	7-15
	7 m tree, shale, Kirstenbosch	O	20	6-43	6-20
<i>Diastella buekii</i>	2 yr cutting, sandy loam, Kirstenbosch	S,O, O/C,C	10	3,5-35	6,5-13
<i>D. proteoides</i>	Mature shrubs, fine sand, Pella	S,O,O/C	8	5-39	5-22
<i>D. serpyllifolia</i>	3,5 yr shrublet, rocky sandstone, Bot River	S,C,O/C	7	6,5-29	4-13,5
<i>Faurea macnaughtonii</i>	2 yr cutting, sand-humus mix	S	0	10-16	5-12,5
	1,4 m seedling, humic loam, Knysna forest	S,O/C	2	3-19	4-15
<i>F. speciosa</i>	5 yr shrub, sandy loam, Kirstenbosch	S,O	7	2-21	3,5-12
<i>Leucadendron argenteum</i>	3 m tree, sandy loam, Kirstenbosch	S,O	28	3-66	5-13
<i>L. discolor</i>	9 mth seedlings, sand-humus mix	S	0	5-20	—
<i>L. eucalyptifolium</i>	9 mth seedlings, sand-humus mix	S,O	—	5-30	—
<i>L. floridum</i>	6 yr shrub, laterite ^o	S,O	—	—	—
	2 yr cuttings, sand-humus mix	S,O	6	2,5-27	2,5-17
<i>L. galpinii</i>	3 yr shrub, coarse sand	S,O ^o	—	—	—
<i>L. laureolum</i>	10 mth potted seedlings, fine sand, Pella	S,O, C,O/C	12	3,5-40	2,3-18
	13 yr shrub, rocky sandstone, Bot River	S,O,O/C	24	3-60	4-20
<i>L. muirii</i>	3 yr shrub, coarse sand ^o	O	—	—	—
<i>L. salicifolium</i>	10 mth seedlings, sand-humus mix	S	0	—	—
	2 yr seedlings, sandstone, Bainskloof	S	0	30	10
<i>L. salignum</i>	5 yr regrowth, fine sand, Pella	S,O	—	—	—
	2 yr seedlings, coarse sand ^o	S,O/C	—	—	—
<i>Leucospermum cordifolium</i>	2 yr cuttings, sand-humus mix	O,C, O/C	7	6-31	4-13
	2,0 m shrubs, stony sand, base Table Mt	S,O, C,O/C	40	2,5-75	3,5-15
<i>L. conocarpodendron</i>	2 yr cuttings, sand-humus mix	O,C, O/C	27	2,5-21	3-11
<i>L. hypophyllocarpodendron</i>	Mature rhizomes, fine sand, Pella	O,C, O/C	10	5-35	5-29

Species	Specimens	Description of proteoid roots			
		Type ⁺	No. of 2°rts*	Length (mm)	Width (mm)
<i>L. parile</i>	Mature shrubs, fine sand, Pella	S,O,O/C	20	29-54	10-34
<i>L. truncatulum</i>	2 yr seedlings, coarse sand ^o	S,O,C	—	10-30	6
<i>Mimetes cucullatus</i>	2 yr cuttings, sand-humus mix	S,O, C,O/C	8	4-22	3,5-15
<i>M. hirtus</i>	2 yr cuttings, sand-humus mix	S,O,C	9	4-31	4-17
<i>Orothamnus zeyheri</i>	2, 5 yr seedling, potted sand	S,O,C	5	1,5-31	6-13
<i>Paranomus reflexus</i>	600 mm cutting, loamy sand, Kirstenbosch	S,O,C	7	4-22	2-8
<i>P. spicatus</i>	2 yr cuttings, sand-humus mix	S,O,O/C	7	2-22	4-9
<i>Protea acaulos</i>	Mature rhizomes, fine sand, Pella	S,O,O/C	7	8-34	7-23
<i>P. nitida</i>	2 m tree, sandstone, Bainskloof	O	4	10-25	10-15
<i>P. aurea</i>	3 yr shrub, coarse sand ^o	O	—	—	—
<i>P. burchellii</i>	2 m shrub, fine sand, Pella	C	6	50	30
<i>P. cynaroides</i>	2 yr seedlings, sand-humus mix	S,O,C	9	2-6	4-13
<i>P. discolor</i>	3 yr seedlings, coarse sand ^o	S,O	—	—	—
<i>P. laurifolia</i>	2 yr seedlings, sandstone, Bainskloof	S	0	—	—
<i>P. magnifica</i>	3 yr seedlings, coarse sand	O	—	—	—
<i>P. neriifolia</i>	2,5 m shrub, fine sand, Kirstenbosch	S,O,C	17	2-36	3-17
<i>P. repens</i>	1 m shrub, fine sand, Pella	S,O,O/C	35	5-53	2-17
<i>P. speciosa</i>	18 mth seedlings, coarse sand ^o	O	—	—	—
<i>P. stokoei</i>	12 mth seedling, coarse sand ^o	S,O	—	—	—
<i>Serruria aitonii</i>	2 yr cuttings, sand-humus mix	S,O, C,O/C	13	4-30	3-19
<i>S. burmannii</i>	Flowering shrublet, fine sand, Pella	S	0	25	8
<i>S. ciliata</i>	2 yr cuttings, sand-humus mix	S,O	7	3-19	3-11
<i>S. elongata</i>	3 yr cuttings, sand-humus mix	S	0	3-15	2-10
<i>S. florida</i>	2 yr cuttings, sand-humus mix	S,C,O/C	6	7-32	4-13

Species	Specimens	Description of proteoid roots			
		Type ⁺	No. of 2° rts [*]	Length (mm)	Width (mm)
<i>S. pedunculata</i>	3 yr shrub, coarse sand ^o	S	0	—	—
<i>S. simplicifolia</i>	2 yr seedlings, fine sand, Pella	S	0	10–20	5
<i>S. vallis</i>	2 yr cuttings, sand-humus mix	S	0	3–29	6–16
<i>Sorocephalus lanatus</i>	2 yr cutting, brown sand, Kirstenbosch	S	0	4–17	2–5
<i>S. capitatus</i>	1,5 yr cuttings, sand-humus mix	S,O	4	3,5–36	3,5–17
<i>Spatalla incurva</i>	2 yr cutting, brown sand, Kirstenbosch	S,O	—	2–23	1,4–7
<i>S. parilis</i>	2 yr cutting, brown sand, Kirstenbosch	S,O	—	2–19	1,5–6
<i>S. racemosa</i>	5 yr shrublet, rocky sand-stone, Bot River	S,O	3	1,5–20	1,5–9

⁺ S = simple proteoid roots, O = open compound, C = closed compound, O/C = incompletely open or closed, letter in italics = most proteoid roots of this type

^o Cultivated plants in Perth, Western Australia

^{*} Maximum number of second-order roots within a compound proteoid root bearing simple proteoid roots

Note: Length and width measurements refer to simple proteoid roots, even when these are components of compound proteoid roots.

Ontogenetically, and perhaps phylogenetically (Johnson and Briggs, 1975), the results suggest that compound proteoid roots are more “advanced” than simple types. Compound proteoid roots with many branches are more advanced than those with few branches. Closed are more advanced than incompletely-closed, which are more advanced than incompletely-open, which are more advanced than open. Similarly, compound proteoid roots with higher order clusters, are more advanced than those with lower order clusters.

All proteoid roots were made up of two (some *Paranomus reflexus* roots) to six (some *Leucadendron argenteum* roots) longitudinal rows of rootlets, as found for the genus *Hakea* in Australia (Lamont, 1972a). Proteoid rootlets varied in average width from 80 μm (*Sorocephalus lanatus*) to 250 μm (e.g. *Faurea speciosa*). These dimensions are much less than those for rootlets of *Protea neriifolia* developed in tissue culture (1,5–5 mm) and claimed to be proteoid (van Staden *et al.*, 1981). Their approximate length can be

determined by dividing width of proteoid roots in Table 1 by two. Most rootlets were in single rows (Fig. 1C), but those of *Mimetes cucullatus* and *M. hirtus* were in double rows due to compaction displacing alternate rootlets sideways (illustrated in Lamont, 1972a and to some extent in Fig. 1B). *Leucospermum hypophyllocarpodendron* was unusual in possessing some proteoid roots with non-contiguous "incomplete" rootlets (Table 5). The number of rootlets per unit axis length varied from 60 (*L. argenteum*) to 140 (*S. lanatus*) per 10 mm row, depending on diameter and arrangement of the rootlets (Table 5). Including all rows, this gives about 200 rootlets/10 mm axis length for ten-month seedlings of *Leucadendron laurum* to 650 rootlets/10 mm axis length for typical proteoid roots of rooted cuttings of *M. cucullatus*. The root hairs on proteoid rootlets were often much longer than those on non-proteoid roots (compare Fig. 1C and D), ranging from 250 μm (*Serruria aitonii*) to 725 μm (*L. hypophyllocarpodendron*).

In an experiment with *Leucadendron laurum* (Lamont, unpubl.), mature proteoid roots had 2.6 times the surface area per unit dry weight as adjacent non-proteoid roots, omitting any contribution by root hairs. The root hairs on proteoid rootlets were three times the length of those on non-proteoid roots (though of similar width and density). This gave an additional 5.84 mm² of surface per 1 mm² of epidermal surface, 2.6 times that of equivalent non-proteoid roots. The total root surface of mature proteoid roots per unit weight was consequently 5.4 times that of mature non-proteoid roots. This is consistent with Jeffrey's (1967) claim of 4.5 times for *Banksia ornata*, though the dense cover of root hairs on the proteoid roots of other species (e.g. *Brabejum stellatifolium*, *Faurea macnaughtonii*, *Protea cynaroides*) would greatly increase this figure.

Contribution to the root system

Nine months after germination, pot-grown *B. stellatifolium* had no proteoid roots, while they were abundant in *Aulax cancellata*, *A. umbellata*, *Leucadendron eucalyptifolium* and *L. laurum* (Table 2). The delay in proteoid root initiation in *B. stellatifolium* was no doubt due to the large store of nutrients in the still-intact drupe. The smaller cotyledons on the other species, except *Aulax umbellata*, had already decayed. That commencement of proteoid root initiation is not necessarily tied to cotyledon abscission however (Lamont, 1972a) is confirmed by *A. umbellata* (and *Protea cynaroides*, Table 4), which had the greatest concentration of proteoid roots. As indicated by *Leucadendron*, there was as much variation in concentration of proteoid roots in the root systems between species in a given genus as there was between genera (see also Table 4). At this early stage in growth, there was also much variation in proteoid root production between

TABLE 2.

Production of proteoid roots by six pot-grown species of Proteaceae in relation to shoot and total root growth, nine months after germination. Results are mean $\pm$ standard deviation for six plants, except *Leucadendron discolor* (twelve plants). Significant curvilinear correlations between number of proteoid roots and plant weight are indicated.

Species	Shoot wt (g) (A)	Root wt (g)	No. proteoid rts/plant (B)	No. proteoid rts/g root wt	Correl. A v B
<i>Aulax cancellata</i>	0,79 $\pm$ 0,15	0,34 $\pm$ 0,10	22 $\pm$ 20	65 $\pm$ 71	NS
<i>A. umbellata</i>	1,05 $\pm$ 0,32	0,47 $\pm$ 0,15	72 $\pm$ 78	134 $\pm$ 122	*(linear)
<i>Brabejum stellatifolium</i>	1,81 $\pm$ 0,66	1,59 $\pm$ 0,86	0 $\pm$ 0*	0 $\pm$ 0	NS
<i>Leucadendron discolor</i>	1,02 $\pm$ 0,24	0,44 $\pm$ 0,14	4 $\pm$ 6	8 $\pm$ 10	NS
<i>L. eucalyptifolium</i>	2,26 $\pm$ 0,37	1,20 $\pm$ 0,22	94 $\pm$ 56	74 $\pm$ 34	*(log)
<i>L. laureolum</i>	3,08 $\pm$ 0,64	1,05 $\pm$ 0,39	50 $\pm$ 26	47 $\pm$ 17	NS

* One plant with one proteoid root; NS not significant; *significant at 5 % level.

TABLE 3.

Growth of *Leucadendron discolor* nine months after germination in relation to six plants with proteoid roots and six without. Results of tests of significance are given.

	No. proteoid roots	Total plant wt	Shoot wt	Root wt
	0 $\pm$ 0	1,41 $\pm$ 0,29	1,08 $\pm$ 0,27	0,44 $\pm$ 0,12
	8 $\pm$ 4	1,52 $\pm$ 0,36	0,97 $\pm$ 0,20	0,45 $\pm$ 0,10
	***	NS	NS	NS
Sig. Test	Mann-Whitney	Anovar	Anovar	Anovar

TABLE 4.

Contribution by new season's proteoid roots to the root systems of two-year-old pot-grown plants of eight species in six genera. Results are mean $\pm$ standard deviation for three replicates.

	Shoot wt (g) (A)	Root wt (g) (B)	Ratio A/B	No. proteoid rts/g total wt ^a	% proteoid rt wt/ total rt wt	Wt per proteoid rt (μ g)
<i>Leucadendron floridum</i>	3.35 $\pm$ 0.87	0.70 $\pm$ 0.44	4.8	176 $\pm$ 33	20.2 $\pm$ 7.1	1.1 $\pm$ 0.3
<i>Leucospermum formosum</i>	7.08 $\pm$ 1.13	1.43 $\pm$ 0.44	5.0	249 $\pm$ 153	12.7 $\pm$ 6.6	0.6 $\pm$ 0.1
<i>L. oleifolium</i>	6.57 $\pm$ 0.61	1.06 $\pm$ 0.34	6.2	18 $\pm$ 11	2.6 $\pm$ 2.2	1.3 $\pm$ 0.4
<i>Mimetes hirtus</i>	3.40 $\pm$ 1.13	1.02 $\pm$ 0.39	3.3	122 $\pm$ 30	26.3 $\pm$ 9.6	2.1 $\pm$ 0.3
<i>Paranomus spicatus</i>	2.90 $\pm$ 0.10	1.03 $\pm$ 0.08	2.8	121 $\pm$ 42	14.6 $\pm$ 1.8	1.3 $\pm$ 0.3
<i>Protea cynaroides</i> ⁺	1.27 $\pm$ 0.40	0.40 $\pm$ 0.06	3.2	272 $\pm$ 74	29.7 $\pm$ 2.7	1.1 $\pm$ 0.3
<i>Serruria altonii</i>	7.28 $\pm$ 0.84	1.87 $\pm$ 0.54	3.9	92 $\pm$ 20	17.0 $\pm$ 6.5	1.8 $\pm$ 0.3
<i>S. valleria</i>	2.01 $\pm$ 0.61	0.43 $\pm$ 0.12	4.7	39 $\pm$ 6	10.0 $\pm$ 1.3	2.7 $\pm$ 0.3

⁺ Ten month seedlings with cotyledons still present; other species grown from cuttings.

replicates, as suggested by the high standard deviations. Proteoid root concentration in the rooted cuttings from mature plants (Table 4) was much more stable. The greater the number of proteoid roots in the root system of replicates, the higher the proportion of compound ones, suggesting physiological advancement of these plants (see earlier comments on Table 1).

Correlations (linear, logarithmic, exponential, power) between dry shoot weight and number of proteoid roots per seedling, were only significant for two of the six species. In functional terms, then, increased occurrence of proteoid roots cannot be held responsible for instances of greater plant growth in four of the six species. The two positive correlations can even be interpreted as the reverse—larger plants, under otherwise identical conditions, are more likely to have proteoid roots (Lamont, 1981a).

Advantage was taken of the absence of proteoid roots in six plants of *Leucadendron discolor* to compare their growth against six plants with them (Table 3). Again, those with proteoid roots were not larger than those without them. This is no doubt due, at this young stage, to lack of dependence on external supply of nutrients and too recent formation of proteoid roots. Variations in seed size, date of germination and soil attributes (nutrients, air and water availability, stimulatory bacteria, see Lamont, 1981a) between replicates could explain the apparent random fluctuations in occurrence of proteoid roots between plants.

Of seven species of rooted cuttings, only *Serruria aitonii*, *S. vallis* and *Leucospermum oleifolium* had <100 new season's proteoid roots/g total root weight (Table 4). The root systems of cuttings can be regarded as equivalent to new season's growth of mature plants, since these also are invariably of adventitious origin (Lamont, 1972a). *L. oleifolium* was the only species of the seven in flower (mid-March), had the fewest proteoid roots and yet the highest shoot/root ratio. Reproductive growth may well compete with root growth in this species and phenological studies might be informative. *L. formosum* on the other hand had greatest concentration of proteoid roots, up to 440/g total dry root weight in one replicate. This compares favourably with the other highest records of proteoid root abundance: 354 for one *P. cynaroides* seedling (Table 4), 557 for portion of the root system of an 18-month *Leucadendron laurum* in humus-rich soil (Lamont, unpubl.) and 578 for a surface lateral of a 3 m high *L. argenteum* at Kirstenbosch.

Proteoid roots were not weighed individually, but ranged from an average weight of 0.5 mg (*Leucospermum formosum*, mostly immature) to 3.0 mg (*Serruria vallis*) throughout the root system (Table 4). For comparison, proteoid roots in *Leucadendron laurum* seedlings of similar age weighed on average 7.3 mg in Clovelly sand (Table 7). There was some tendency for species with a greater number of proteoid roots to have smaller

ones on average (Table 4). This was apparently due to an increased proportion of compound proteoid roots with higher order (i.e. smaller) laterals bearing most of the (consequently smaller) simple proteoid root components (see Fig. 2b and Table 1).

The contribution of living proteoid roots by weight to the total root system varied from 1 % (*L. oleifolium*) to 37 % (*Mimetes hirtus*) (Table 4). Proteoid roots (including dead) accounted for 80 % of the dry weight of the surface lateral of the specimen of *L. argenteum* noted above. If proteoid roots increase the efficiency of nutrient uptake (Jeffrey, 1967; Malaczuk and Bowen, 1974; Lamont, 1982) then a positive correlation between % weight of proteoid roots in the root system and shoot/root ratio might be expected. That is, as the % contribution of proteoid roots increases, proportionately more shoot weight should be supported. No such simple, mechanical relationship is evident between replicates or species in Table 4. The reason is that growth is as much dependent on initial plant nutrient status and species recycling ability (Grundon, 1972) as on root morphology.

Factors affecting formation

Age. After nine months, all pot-grown seedlings of *Aulax umbellata*, *Leucadendron eucalyptifolium* and *L. laureolum* had proteoid roots in abundance (Table 2), but only half of *L. discolor* and no *B. stellatifolium* had them. Study of the two *Leucadendron* species over time (Fig. 3) shows absence of proteoid roots up to 17 weeks. By about 25 weeks all seedlings possessed them. *L. laureolum* shows a power function increase in number of proteoid roots with increase in shoot growth (r sig. at 1 % level). As discussed earlier, it is not possible to unravel cause and effect from such data. It is clear, however, that the older the plant the more likely it is to have proteoid roots, and that by the second year of growth they are standard components of the root systems of these species (also see Table 1).

Soil type. Nine-month seedlings of *Leucadendron laureolum* grown in Clovelly-type soil (fine sand) had almost 50 % more, and larger, proteoid roots than those in Hutton-type soil (clay-loam) (Fig. 4). This was partly attributable to the fact that root weight in Clovelly soil was twice that in the Hutton, despite the fact that the Clovelly soil had only one-third the level of extractable phosphate as the Hutton (C. Brown, unpubl.). It is possible that phosphate was at inhibitory levels in the Hutton, although in other species proteoid root production ceases altogether at levels which inhibit "normal" root growth (Lamont, 1972b). In view of the high water content of the potted Hutton soil (Lamont, unpubl.), the results are more consistent with the effects of mild waterlogging on root growth as demonstrated for other proteaceous species (Lamont, 1976).

TABLE 5.

Distribution of recently-emerged proteoid rootlets along the parent axis. Double rows result when alternate rootlets are displaced laterally as they emerge. Contiguous rootlets lack gaps between them within the longitudinal row. Incomplete rows have gaps exceeding diameter of rootlets within the axis.

	Specimen	Rootlet arrangement	No. rtlets/row /10 mm axis
<i>Diastella proteoides</i>	Table 1	Single row, contiguous, complete	75
<i>Leucadendron argenteum</i>	Table 1	Single row, contiguous, complete	60
<i>L. floridum</i>	Table 4	Single row, contiguous, complete	90
<i>L. salicifolium</i>	Table 2, Fig. 1	Single row, contiguous, complete	100
<i>Leucospermum formosum</i>	Table 4	Single row, contiguous, incomplete ⁺	80
<i>L. hypophyllocarpodendron</i>	Table 1	Single row, non-contiguous ⁺ , incomplete ⁺	75
<i>Mimetus cucullatus</i>	Table 1	Double row, contiguous, complete	130
<i>M. hirtus</i>	Table 4	Double row, contiguous, complete	75
<i>Serruria aitonii</i>	Table 3	Single row, contiguous, complete	140
<i>Sorocephalus lanatus</i>	Table 4	Single row, contiguous, complete	140
<i>Spatalla parilis</i>	Table 4	Single row, contiguous, complete	100

⁺ This condition not common

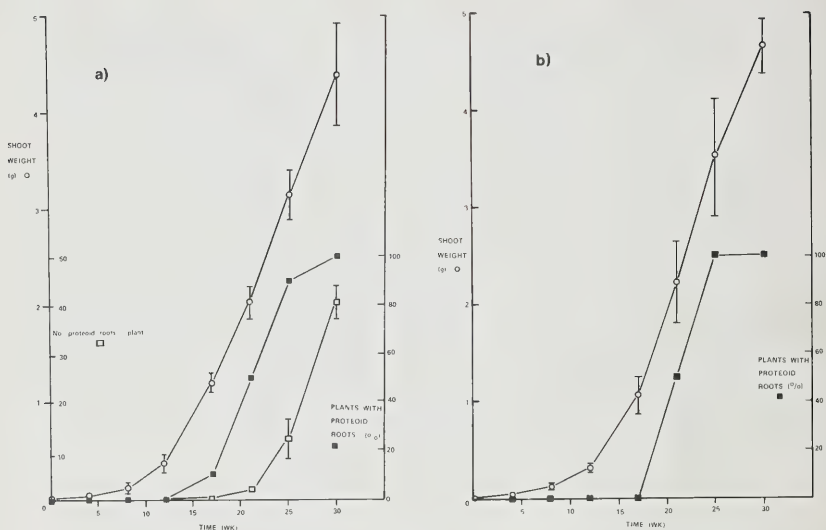


FIG. 3.

Presence of proteoid roots in relation to age of seedlings of *Leucadendron laurifolium* (a, ten plants at each harvest) and *L. eucalyptifolium* (b, seven plants). Mean $\pm$ standard errors are given. O—shoot dry wt, ■—% plants with proteoid roots, □—no. proteoid roots per plant.

Soil profile distribution. Examination of many plants in a range of soil types (Table 1) repeatedly confirmed that the proteoid roots were concentrated in the uppermost 100 mm of soil, especially in the decomposing litter and humus layers beneath the canopy of the plant, as found in Australia (Lamont, 1973). The abundance of compound proteoid roots in larger and older plants (Table 1) resulted in a distinct mat of proteoid roots just under the raw litter (e.g. *Leucadendron salignum* and *Protea burchellii* at Pella) though this only remained continuous under the plant canopy, unlike *Banksia* in Australia which may extend between plants (Jeffrey, 1967). The results for adult plants of *Leucospermum parile* at Pella will be described elsewhere (S. Jongens-Roberts and D. T. Mitchell, unpubl.), but preliminary data for two-year-old plants (Table 6) show that the pattern is established early. In this case, there was no decomposing litter layer and 90 % of all proteoid roots were concentrated in the uppermost 50 mm of soil. Both proteoid root number and weight fell away exponentially with depth, with

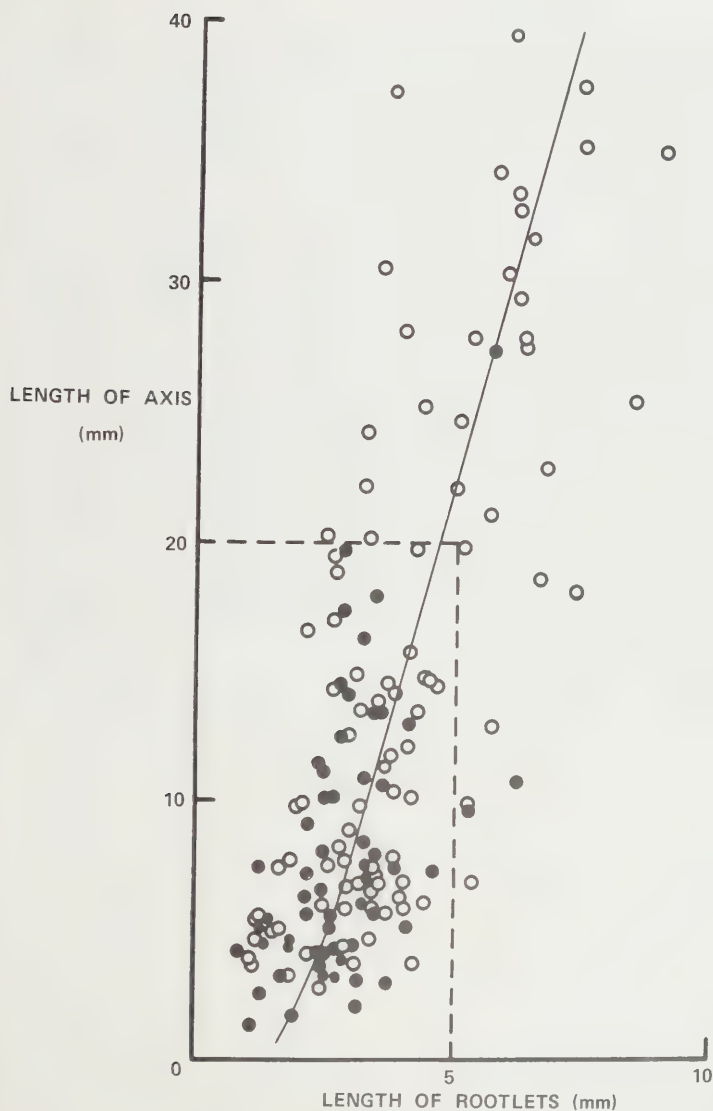


FIG. 4
 Dimensions of proteoid roots of *L. lauroolum* in one plant grown in Clovelly sand (○) and one in Hutton clay-loam (●) for nine months. Note the essentially linear relationship between axes and rootlet lengths, and the paucity of large proteoid roots in the Hutton soil. Part of the wide variation about the best-fit line is due to inclusion of immature proteoid roots.

none below 150 mm. This pattern was in no way related to the distribution of lateral roots which remained fairly constant down to 600 mm, nor to soil water availability which increased below 300 mm (Table 6). There was a linear, rather than exponential, drop in soil organic matter with depth but, together with the nutrients released from the fire that initiated germination, the proliferation of proteoid roots at the surface can be related to enhanced nutrient availability here (Lamont, 1973).

Seasonality. The root systems of thirteen species examined in the field (Kirstenbosch, Bainskloof, Kogelberg Mts and Pella, see Table 1) during March 1980 usually only possessed dead proteoid roots. The rootlets were brown, broken off or lacked cortices or root hairs. The exceptions were plants of *Leucospermum hypophyllocarpodendron* examined in Clovelly sand at Pella on 3rd and 18th March, 1980. Some of the adventitious roots arising from the rhizomes possessed young and mature compound proteoid roots. The rootlets were white and densely-covered with root hairs (Tables 1, 5). The rhizosphere soil had a water content of 3,34 % (above field capacity of 2,4 %), while the surrounding soil had a water content of 0,34 % (below permanent wilting point of 1,8 %). One explanation is that dew rolled down the vertically-oriented leaves, over the rhizome and down the parent root to create a locally-moist environment for root growth. In view of the small surface area of these leaves, the hydrophobicity of this soil when dry, and the unreliability of such a source for ongoing root growth, this possibility seems remote. Active roots are quite capable of releasing water on the other hand (e.g. Lamont, 1981b), and a more likely explanation is that water was provided from the sub-soil via the massive taproot and released into the rhizosphere. By maintaining a moist rhizosphere these "anomalous" summer proteoid roots may serve to prolong nutrient release from the organic particles and take advantage of "out-of-season" showers (Lamont, 1982).

Following the first substantial autumn rains at Pella both "normal" and proteoid root growth commenced in *Leucospermum parile* at least (Table 7). By mid-June there was vigorous proteoid root growth at the same site by *Diastella proteoides* (flowering), *Leucadendron salignum*, *Protea repens* and *P. burchellii* and to a lesser extent *Serruria simplicifolia*. October appeared to be the critical month for cessation of proteoid root growth (Table 7). By mid-October, the surface soil around fifth-year plants of *Protea repens* and *P. burchellii* was dry and all roots were moribund. Under 20-year stands of these species however, with a thick layer of litter and canopies to the ground, the soil was still moist and young and mature proteoid roots were abundant. By late October proteoid root growth here had also ceased. However, excavations around *P. neriifolia*, *Leucadendron argenteum* and *Leucospermum conocarpodendron* at Kirstenbosch over summer showed growth

TABLE 6.
Distribution of roots through the soil (Clovelly-type) profile of two-year-old plants of *Leucospermum parile* at Pella (via Atlantis) on 2 June 1980

Soil* Depth (mm)	No. of proteoid roots	Wt of proteoid roots	Wt of laterals	Wt of tap root	Soil water content (%)	Organic matter (%)
0-50	90	0.31	0.17	0.87	2.08	1.96
50-100	8	0.03	0.07	0.30	1.91	1.65
100-150	1	0.02	0.08	0.31	1.64 ^ø	1.43
150-300	0	0.00	0.10	0.37	1.62 ^ø	1.13
300-450	0	0.00	0.12	0.16	2.42	0.86
450-600	0	0.00	0.13	0.04	2.78	0.74

* soil core 250 mm diameter centred on base of plant.
ø below water content at 15 bar suction.

TABLE 7.
Seasonality of proteoid root growth related in general terms to that of other organs for four-year plants of *Leucospermum parile* at Pella (via Atlantis)

Date (1980)	Shoot growth	Reproductive growth	Root growth	
			Non-proteoid	Proteoid
3 March	+	-	-	-
1 April	+	-	-	-
13 May	+	-	+	+
2 July	-	+	+	+
21 October	-	++	+	++
31 October	+	+	-	-
12 December	++	-	-	*

- = no growth, + = moderate growth, ++ = maximum growth
* a few moist clusters present.

of both types of roots continued provided the soil remained moist (e.g. 5.9 % water content recorded beneath *L. conocarpodendron*). Examination of *Leucadendron laureolum*, *Diastella serpyllifolia* and *Spatalla racemosa* at Bot River on December 10 showed all surface roots to be dormant. Clearly, where surface water availability is highly seasonal so also is root growth, including production of proteoid roots, as previously demonstrated in a related mediterranean ecosystem (Lamont, 1976).

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